REVISION OF THE *AMPHIBOLURUS DECRESII* COMPLEX (LACERTILIA: AGAMIDAE) OF SOUTH AUSTRALIA

by T. F. HOUSTON*

Summary

HOUSTON, T. F. (1974).—Revision of the *Amphibolurus decresii* complex (Lacertilia: Agamidae) of South Australia. *Trans. R. Soc. S. Aust.* **98** (2), 49-60, 31 May, 1974.

The taxonomy of the rock-dwelling dragon-lizards of the *Amphibolurus decresii* complex is revised. Two previously established taxa, *A. decresii* (Duméril & Bibron) and *A. fionni* Procter, are tentatively maintained as species while a third species, *A. vadnappa*, is described as new. Each species is composed of two to several races distinguishable mainly on the basis of male coloration. Strict preference (except perhaps in juveniles) for rocky cover and past changes in the distribution of rock outcrops are presumed to have been major factors in evolution of the complex.

Introduction

The species-complex dealt with here includes the Tawny Dragon, *Amphibolurus decresii*, the Peninsula Dragon, *A. fionni*, and several forms hitherto undescribed. The lizards inhabit an area of South Australia bounded by Ceduna in the west, Marree in the north and Kangaroo I. in the south, and which extends east to Mootwingee in western New South Wales (Fig. 1).

Much confusion has arisen around the complex and the need for a taxonomic revision has long been felt. A wide array of colour patterns occurs amongst adult males from different areas with little or no corresponding morphological diversity and without comparable colour variation in females and juvenile males. Thus, while the geographical origin of an adult male may be determined from its colour pattern, this is seldom possible with females or juvenile males. Unfortunately, the name *A. fionni* was based only on the female sex and no accurate indication of the type locality was given. The description fitted females from most areas and the applicability of the name to a particular male colour form was left in doubt. The status and nomenclature of the different male colour forms were variously interpreted with resulting confusion in collections.

The present study included examination of over 300 specimens in the collection of the South Australian Museum and field observations in many parts of South Australia. It has become clear, however, that a full understanding of the complex cannot be obtained without detailed behavioural and ecological studies. This paper is intended to clarify nomenclature as far as presently possible, to facilitate such studies now being undertaken elsewhere.

All specimens listed in this paper are in the South Australian Museum and, unless otherwise indicated, all localities mentioned are in South Australia.

Diagnosis of A. decresii complex

Lizards of moderately to strongly depressed form, up to 25 cm long (snout-vent length ≤ 96 mm); nostril below a sharp canthus rostralis; a weak nuchal crest but no vertebral crest (at most, a line of perfectly aligned keels or a raised fold of skin); dorsal body scales mostly homogeneous, smooth to obtusely keeled and subtubercular; skin around tympani, nape and sides of neck with few to many spines, occurring singly or clustered on folds of skin; ventral scales smooth; 32-50 femoral and preanal pores, closely arranged along a more or less straight line extending full length of thighs but interrupted medially; each pore situated between several scales; lower jaw with dark irregular reticulations or longitudinal lines (often obscured by bright colour washes in males); chest of subadult and adult males with a grey to black patch tapering posteriorly.

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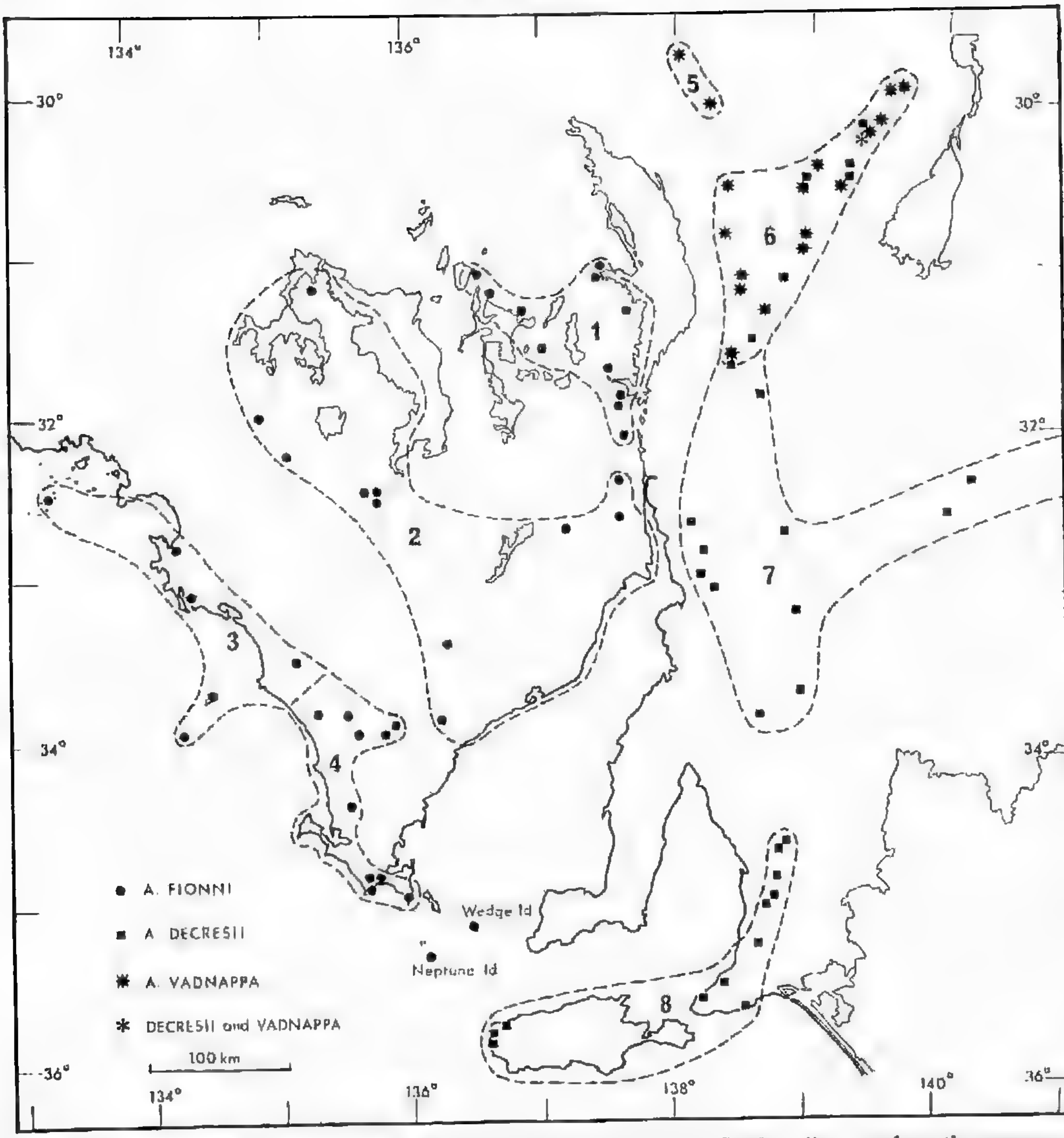


Fig. 1. Distribution of *Amphibolurus decresii* complex in S. Aust. Broken lines enclose the ranges of individual races. The numbers are referred to in the text.

sometimes closely approaching vent; males (except early juveniles) usually with bright yellow, orange, red, pink or blue patches or washes; females and early juvenile males usually dull grey, brown or reddish brown with black stippling and mottling; tail length 1.4–2.3 times snout-vent length; hind limb 0.7–1.0 times snout-vent length.

Examination of all available material suggests the existence of three major taxa (each composed of two to several minor taxa) which I am treating as species. These taxa are distinguishable mainly on colour differences but there are also some minor structural features separating them. The name *A. decresii* (Duméril & Bibron) applies to one taxon (inhabiting areas 6–8, Fig. 1) and the name *A. fionni* Procter to another (inhabiting areas 1–4, Fig. 1, and Neptune and Wedge Is.). In view of the very close similarity of these two taxa, they may not be reproductively isolated, but until this is clearly demonstrated nomenclatorial changes are unwarranted. The third major taxon (inhabiting areas 5 and 6, Fig. 1) is the most distinctive of the three and is partially sympatric with *A. decresii*. In the absence of known intermediates, it is accorded species status and named here as *A. vadnappa.*

It is not a simple matter to clearly define the three forms because of intraspecific variation, but the following key should facilitate recognition of them.

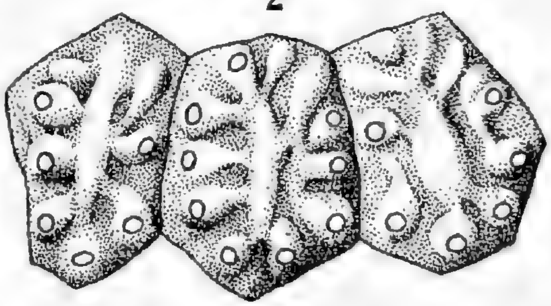
Key to species of the A. decresii complex

1. Dorsal head scales between and in front of eyes usually coarsely wrinkled (Fig. 2), not simply keeled; mid-dorsal row of scales with longitudinally aligned keels extending at least partway along back (more prominent in males which are able to raise a fold of skin along vertebral line); adult males with orange or reddish spots on sides of body tending to coalesce to form vertical bars and with a broad immaculate vertebral stripe from nape to base of tail (Figs. 12, 13); mottling on sides of females often suggestive of barring .... *A. vadnappa*
1. Dorsal head scales between and in front of eyes longitudinally keeled (Fig. 3), sometimes obtusely so or virtually smooth but (Neptune I. specimens excepted) never coarsely wrinkled; no mid-dorsal row of scales with longitudinally aligned keels along back (at most a short incomplete row in some *A. decresii*); adult males without orange or reddish spots on sides of body coalescing into vertical bars or, if so, then maculations extending across vertebral region (Fig. 11); mottling on sides of female variable .... 2.
   2. Sides of body with a few to many scattered tubercles which are usually pale and contrast with ground colour; body colour pattern of adult male consisting essentially of a blackish lateral stripe each side, margined above and below by paler lines or rows of spots; lower jaw of adult male usually bright yellow, orange, or blue .. *A. decresii*
   2. Sides of body without scattered tubercles; body colour pattern of adult male consisting essentially of pale spots or blotches often aligned transversely, sometimes large and coalescing into bars, sometimes reduced and limited mainly to dorsolateral folds; lower jaw of adult male usually with bright yellow wash over greyish reticulations but never with bright blue wash .... *A. fionni*

Amphibolurus decresii (Duméril & Bibron)
FIGS. 1, 4, 14-16

Grammatophora decresii Duméril & Bibron, 1837: 472-4; 1854, pl. 41, figs. 1, 1a-c.
Agama decresiensis Fitzinger, 1843: 83 (new name for *G. decresii* D. & B.).
Ctenophorus decresii (D. & B.), Fitzinger, 1843: 18, 83.
Amphibolurus decresii (D. & B.), Peters, 1864: 229.

Types: Ile de Decres (= Kangaroo I., S. Aust.), collected by Peron and Lesueur. Duméril & Bibron apparently had several specimens of both sexes but did not designate one as the type. They figured a male. Guibé



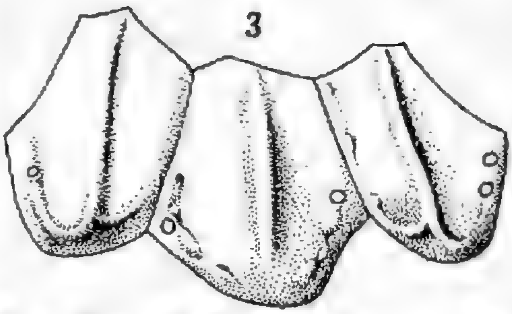


Fig. 2. Three scales from top of snout of *Amphibolurus vadnappa.*
Fig. 3. Same from *A. fionni.*

(1954) records the presence of two syntypes (no. 6545) in the Muséum National d'Histoire Naturelle, Paris.

Duméril & Bibron's (1854) coloured figure of an adult male *A. decresii* clearly shows a black lateral stripe margined above and below with pale spots and their (1837) description mentions small tubercles sprinkled over the flanks. I have no hesitation, then, in applying the name *A. decresii* to the populations inhabiting areas 6–8 (Fig. 1) which are distinguished by these features.

SOUTHERN (TYPICAL) RACE (Area 8, Fig. 1)

This race appears to be confined to the western end of Kangaroo I., the western scarps and gorges of the southern Mt. Lofty Ranges and the southern margin of Fleurieu Peninsula. It is comparatively uniform throughout this range.

Adult male pattern: Head light brown; lower jaw and lips diffusely bright blue; throat and sometimes shoulders bright yellow; black patch in fold of skin each side of neck usually separated by pale brown from blackish lateral stripes on body.

Female pattern: Ground colour usually dull brown or grey-brown; lateral body stripes often developed as in males but black speckling and mottling variable.

NORTHERN RACE(S) (Areas 6 and 7, Fig. 1)

Males from areas 6 and 7 show far more variation in colour pattern than those of the southern race. However, I have seen too few specimens (particularly live males in full coloration) to know whether the variation is regionally dependent or individual only. The bright colour markings and washes about the head and neck closely resemble those of some *A. fionni* males.

Adult male pattern: Head usually grey or dark dorsally; lower jaw reticulated with grey and suffused with bright yellow or with a large orange patch centrally but never with a bright blue wash; throat yellow or orange; markings about ears, neck, nape and sometimes eyelids orange.

Female pattern: Very similar to that of southern females.

SPECIMENS EXAMINED: AREA 6: Arkaroola HS, R10916; East Painter Gorge, R10940; Echo Camp, Arkaroola Creek, R10917; Mern Merna, R2660; west of Mt. Painter Camp, R10915; Mt. Serle, R5902, R5914; Nooldonnooldoona Waterhole, R10952; North Tusk, Gammon Range, R3942; Paralana Springs, R10938, R10961, R10963; St. Mary Peak, R6004; Wilpena Gorge, R3806; 19 km W of Wirrealpa, R3753; Yudnamutana Creek, R3492, R8760, R10201-2. AREA 7: Burra, R12492; Clare, R2337; Mootwingee, N.S.W., R5194; Mt. Remarkable, R3306, R6379, R9533; near Olary, R12909-10; Pt. Germein Gorge, R12792; Terowie, R2496; 13 km SE of Warcowie via Hawker, R2576; Wilmington, R3724; Wirrabara, R8862. AREA 8: Basket Range, R2834; Encounter Bay, R1686; Fifth Creek, R435; Glen Osmond, R9379-85; Kangaroo Is. (R1189; south side, R9339-40; Harveys Return, R11260; Ravine de Casoars, R3283; West Bay, Flinders Chase, R9341); Montacute, R8802; Normanville, R2881; Onkaparinga Gorge, R5854; 32 km N of Peterborough, R11356-7; Sandy Creek (E of Gawler), R12075; Second Valley, R2505; near Tea Tree Gully, R11358-9; Waterfall Gully, R1461, R2137, R2835

Amphibolurus fionni Procter, 1923: 1075, figs. 4a-c.

FIGS. 1, 3, 5-11, 14-16

Holotype: ♀, coast of the mainland of S. Aust., F. Wood-Jones, in B.M.N.H., London. The late Dr. M. Smyth, Department of Zoology, University of Adelaide, who saw the type, informed me that the accompanying data record it from Pt. Lincoln, S. Aust.

It is unfortunate that the description of this species was based on a female only, for, as mentioned above, females may be virtually impossible to identify with any particular race on the basis of appearance. Procter's description and figure, however, and a photograph of the type (Fig. 10) agree closely with specimens from Eyre Peninsula.

Several distinctive races of this species are described below. Since adult males of all races usually have a dark grey reticulum and yellow wash on the lower jaw and throat, it is not mentioned among the diagnostic features of each race.

NORTHERN RACE (Area 1, Fig. 1)

Area 1 corresponds approximately to what was once a large tableland (Arcoona Tableland) and now consists of the low rolling Andamooka Ranges and series of isolated mesas and tenthills. The lizards inhabit the rocky scarps and stony creek beds.

Adult male pattern: Dorsal ground colour brown grading to blackish brown on neck, shoulders and flanks; irregular, often very dense pale spotting or blotching on nape, neck, shoulders and flanks sometimes coalescing to form vertical bars on sides of body (Fig. 11); at least some, and often most, of spots on flanks orange or reddish, the remainder white.

Female pattern: Dorsal ground colour brown; dark mottling on sides of body frequently tending to form alternating light and dark bars.

This race is very similar in coloration to *A. vadnappa*, although it does not exhibit the distinctly bluish tints found on the body and limbs of males of that species, nor does it have predominantly coarsely wrinkled scales on top of the snout nor a vertebral keel line. Some specimens from the southernmost locality of Area 1 (Uro Bluff) differ very little from those of the central race below.

CENTRAL RACE (Area 2, Fig. 1)

Area 2 includes the southernmost remnants of the Arcoona Tableland, the Gawler, Middleback and Blue Ranges and several smaller ranges and isolated hills.

Adult male pattern: Dorsal surface largely blackish except for brownish head and grey limbs and tail; distinct white spots scattered over back and flanks continuing into orange spots and blotches on shoulders, neck and nape (Fig. 5); eyelids often diffusely orange.

Female pattern: Highly variable; dorsal ground colour in Gawler Ranges specimens reddish-brown to brick red but brown to greyish in other areas; dorsal surface stippled and mottled with black to varying degrees and often pale spotted or ocellate in large specimens.

SOUTHERN RACE (Area 4, Fig. 1)

Area 4 coincides with the south-eastern part

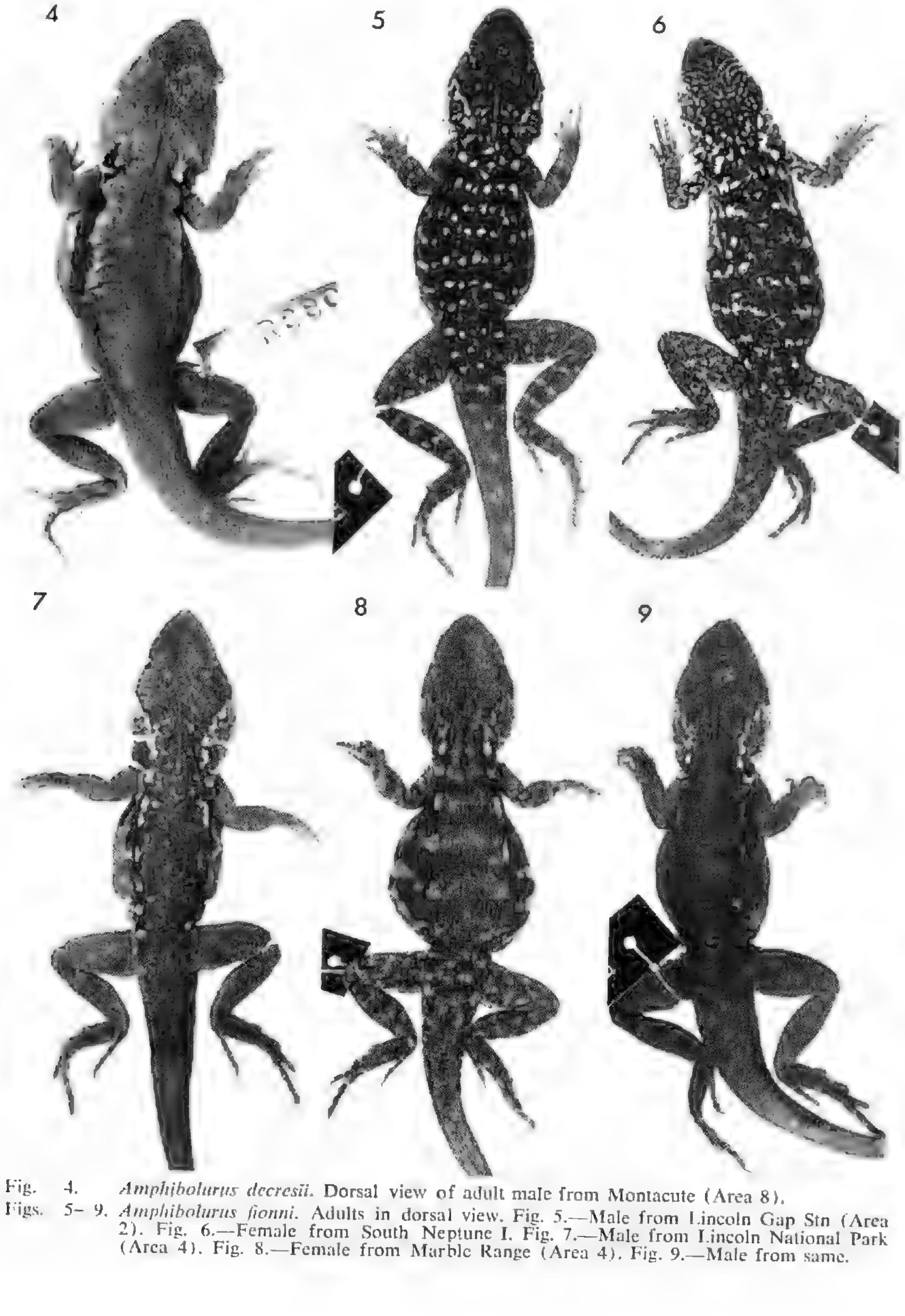


Fig. 4. *Amphibolurus decresii.* Dorsal view of adult male from Montacute (Area 8).

Figs. 5–9. *Amphibolurus fionni.* Adults in dorsal view. Fig. 5.—Male from Lincoln Gap Stn (Area 2). Fig. 6.—Female from South Neptune I. Fig. 7.—Male from Lincoln National Park (Area 4). Fig. 8.—Female from Marble Range (Area 4). Fig. 9.—Male from same.

of a large limestone (calcareous aeolianite) expanse. The limestone is exposed on many rises and has weathered to form numerous rocks and slabs beneath which the dragons find shelter. A number of granitic and gneissic intrusions also occur in the area forming prominent hills with bare rocky outcrops which are also inhabited.

Adult male pattern: Dorsal ground colour pale grey with only a little blackish colour on sides of neck and below dorso-lateral folds anteriorly; pale spotting confined in most specimens to folds of skin about neck and anterior parts of body, especially along dorsolateral folds (Fig. 9), occasionally occurring over back generally but only weakly.

Female pattern: Highly variable; ground colour grey to brown; juveniles often finely speckled but larger specimens usually have dark mottling forming coarse irregular patterns, sometimes with pale spotting. A particularly bold pattern occurs amongst females from the Marble Range (Fig. 8).

This race has been the basis of several reports of *A. decresii* occurring on Eyre Peninsula, because of the similar colour pattern in males of the two forms. However, the absence of scattered single tubercles on the flanks of Eyre Peninsula specimens will distinguish them from *A. decresii*.

Since this race is the only one known to occur in the near vicinity of Port Lincoln, it may be that to which the holotype belongs.[1]

WEST COAST POPULATIONS (Area 3, Fig. 1)

Area 3 includes the northern section of the limestone expanse mentioned above, the Isles of St. Francis and the Investigator Group (Flinders and Pearson Is.). Few male specimens are available from this area so that a clear picture of their variation is not yet available.

Males from Area 3 differ from those of Area 4 in their generally larger size and somewhat bolder colour pattern: the blackish neck patches and lateral body bands are more intense, a pale line or series of spots defines the black neck patches, and enlarged pale spots margin the lateral stripes above and below (Fig. 7). They are even more like males of *A. decresii* than are males of the southern race.

Females tend to have patterning similar to males but in shades of brown rather than grey.

Without further collecting in West Coast localities one cannot be sure that their *A. fionni* populations do not intergrade with those of Area 4.

NEPTUNE AND WEDGE IS. RACES

The populations of these islands differ from those of Area 4 in colour pattern and their generally larger adult size.

Adult male pattern: Dorsal ground colour brown tending to black on neck, shoulders and flanks; scattered distinct white spots on nape, neck, back and base of tail tending to align in transverse rows; blackish coloration intensified around many pale spots on back, almost forming ocelli. Since only preserved specimens were examined, the presence of bright colour washes (other than yellow on the throat) was not observed.

Female pattern: Very similar to male pattern although generally paler with even more distinct ocelli and much black stippling (Fig. 6).

Neptune Is. specimens have conspicuously rougher and more mucronate scales on the base of the tail and hind legs than specimens from Wedge I. and other areas. They are also unusual in that the scales on top of the snout tend to be wrinkled (as in Fig. 2, but not so coarsely). The dorsal snout scales of Wedge I. specimens are mainly smooth.

While the various races outlined above show marked differences from one another in male coloration viewed overall, there is considerable variation within each race and convergence of features may be found in specimens from different races. In view of this, I have preferred not to erect subspecies of *A. fionni*.

SPECIMENS EXAMINED: AREA 1: 3 km SW of Beda Hill, R3877; Bowmans Creek, Bosworth Stn, R3833; north-west tip of Curnapateena Arm of Lake Torrens, R13315; Eucolo Creek, R13323 R13485; eastern side of Lake Hart, R8065-7 south end of Lake Torrens, R3832; 24 km S of Pimba, R6189; Uro Bluff, R12832, R12835-6, R12904; Woodforde Creek, R2795, R2798. AREA 2: Blue Range, R10121, R10173; Carappee Hill, R9313, R12927; Corunna Hill, R12445, R12741; Kondoolka Stn, R12755; Lincoln Gap Stn, R12466-70; Middleback Range, S of Iron Baron, R12929, R13055; Mt. Nott, S of Thurlga HS, R6229-30; Payney Stn, R8804; South Tent Hill, 24 km WNW of Pt. Augusta, R13054; Tandaie Rock Holes, R12592; Thurlga Stn, R5894, AREA 3: 6.5 km S of Baird Bay, R9241-2; Flinders I., R1445; Mt. Wedge, R5732, R5830, R9243; Pear-

[1] Another race was found recently on granite outcrops immediately north of Pt. Lincoln by Mr. J Gibbons, Dept. of Zoology, University of Adelaide. This race, adult males of which are superficially like those of the Neptune I. race in coloration, may equally well be the typical one.

son Is. (R10239, R10833-5; northern island, R10208); St. Francis I., R1196, R3009, R12874; Streaky Bay, R392. AREA 4: eastern edge of Bascombes Well National Park, R12615; Blesing Reserve, R9227-40; near Fishery Bay, R2551; Hincks National Park, R10100; Hundred of Nicholls, R10101, R10103-5, R10107-10, R10113, R10116, R10119; R10178; 19 km NW of Karkoo, R9417; Lincoln National Park, R12924-5, southern end of same, R12926, R13056; Marble Range, R12930; Mikkira HS, R8752-3; 19 km from Sheringa, R3626; Sleaford Mere, R8402; 3 km W of same, R12928, NEPTUNE IS.: R2230, R8722-3; south island, R5351, R5440, R10829-32; north island, R12892, WEDGE I.: R5340, R10636-7, R11375

Amphibolurus vadnappa, sp. nov.

FIGS. 1, 2, 12, 13, 14-16

Holotype: ♂ (R3416B), Aroona Waters (138°21'E, 30°35'S), Flinders Ranges, S. Aust., 3.v.1953, P. F. Lawson.

This species inhabits Areas 5 and 6 (Fig. 1), the type locality being in the latter. Proximity of the range of this species to that of the northern race of *A. fionni* and the remarkably similar coloration of adult males of both forms might suggest that they are merely races of the one species. However, the two may be distinguished on the features outlined in the key. Adult males of *A. vadnappa* also tend to exhibit a bright bluish suffusion of the chin, flanks, and limbs which is not known in northern *A. fionni*. Some differences in body proportions also occur (see below).

This attractive species was well known to Aborigines of the Flinders Ranges from whose language the specific name has been taken. The Aborigines were impressed by the presence of red bars on the males alone and likened males to boys about to be initiated who are painted with red stripes on the back. The females they likened to girls who are never so adorned. They call the lizard 'Itivadnappa' ('iti' = lizard, 'vadnappa' = boy painted for initiation ceremony). (R. W. Ellis, personal communication).

The specific name is used as a noun and is not liable to termination changes.

FLINDERS RANGES (TYPICAL) RACE (Area 6, Fig. 1)

Head and body only moderately depressed (less than the other two species); neck in adult males at least as wide as head so that latter appear to sit directly on shoulders.

Measurements of holotype: Total length, 252 mm; snout-vent length, 79 mm; tail length, 173 mm; hind limb length, 70 mm; head width, 22 mm; snout-gular fold length, 29 mm; total femoral and preanal pores, 43.

Scalation: Scales on top of snout coarsely wrinkled (Fig. 2), seldom almost smooth, never simply keeled as in Fig. 3; folds of skin above and behind ears and on sides of neck with clusters of small spines (feebly developed in juveniles and females); scales of flanks very small, subtubercular and homogeneous, grading into slightly larger, flatter dorsal scales which are very feebly keeled; flanks without scattered single tubercles; a row of perfectly aligned, longitudinally keeled scales extending from nuchal crest about three quarters of length of back (less well-developed in females); this keel line frequently accentuated by being raised on fold of skin.

Adult male coloration: Head pale brown dorsally; broad mid-dorsal stripe from nape to base of tail and upper parts of limbs and tail light grey or blue-grey; sides of neck and body blackish with orange or red spots and blotches usually partly coalesced forming irregular vertical bars (Fig. 12); chest with large diffuse black patch anterior to which skin is bright yellow, the yellow extending onto throat and shoulders and occasionally as spots along flanks; chin and 3–4 longitudinal lines on each side of lower jaw blue or blue-grey; limbs and dark ground colour of flanks slightly to strongly suffused with blue (the yellow, orange, red and, to a lesser extent, blue colorations gradually fade away in spirit).

Female coloration: Dull brown above with coarse dark mottling on sides of neck and body forming a pattern of alternating, irregular, light and dark bars; dorsal surface with scattered blackish spots; lower jaw and throat with longitudinal dark grey lines (more numerous and prominent in juveniles).

WILLOURAN RANGES RACE (Area 5, Fig. 1)

The Willouran Ranges, lying west of the Lyndhurst-Marree road, represent a northwestern spur of the Flinders Ranges system but are isolated by wide tracts of sand and soil plain.

Three males from this area differed from the typical form in their less robust build and narrower necks. The pale spots on their bodies were smaller and while tending to be aligned transversely, did not coalesce to the same degree (Fig. 13).

SPECIMENS EXAMINED: Paratypes—Angepena, 32 km E of, R3423; Arkaroola, R10918-23, R11361, R11373; Aroona Waters, R3416 A and C, R4821; Beltana, R3001; Boulder Bore, R10934-5; Com-

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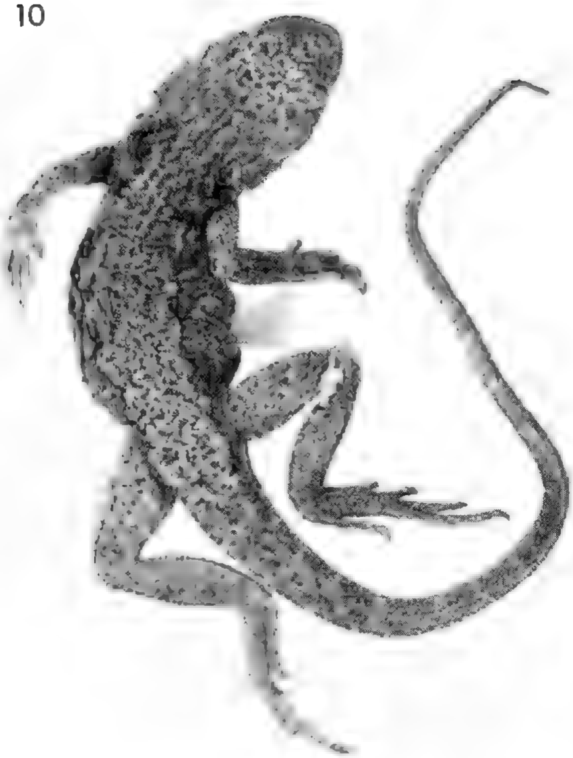

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modore, 9.7 km NE of, R2819; East Painter Gorge, last 8 km of, R10965-7; Echo Camp, Arkaroola Stn, R10946; Illinawortina Pound, R3950; Mt. Aroona, R3314A, B and D; Mt. Fitton, Moolawatana Stn, R8114; Narrina Stn, R10402-4; Oraparinna National Park, R12749, R13053; Parachilna Gorge, R4321; Terrapinna Springs, R12432; Waukawoodna Gap, 96 km N of Blinman, R12837; Yudnamutana Gorge, R3492, R13135; Wilpena Pound, R10638. Allotype—Mt. Aroona, R3314C.

Morpho-metrics

Maximum size

The maximum size attained by adults was found to vary somewhat between races as shown in the following table.

Species or Race	*Maximum snout-vent length in mm* (♂ and ♀)	
A. decresii		
(Northern)	82	73
(Southern)	75	75
A. fionni		
(Northern)	94	82
(Central)	78	72
(West Coast)	85	79
(Southern)	77	76
(Neptune Is.)	96	87
A. vadnappa	82	75

These figures suggest a north-south trend of decreasing body size apart from the Neptune Is. race which attains the greatest body size of all.

Relative length of hind limbs and tail

In this comparison only data from adult and subadult specimens were incorporated, since the relative lengths of appendages decrease slightly with increasing body size (i.e. with age). The lengths of the limbs and tail are expressed as functions of the snout-vent length (SVL). The range and mean for each form is shown graphically in Figs. 14 and 15. Unfortunately, the sample size in some cases is extremely small because of the number of specimens which had broken tails.

A general trend is noticeable towards slightly relatively longer limbs and tails in males (except perhaps in *A. decresii*). While there is wide overlap in the data of each form and the means of most of them approximate, *A. vadnappa* stands out from the rest in its greater mean relative length of both hind limbs and tail.

Femoral and preanal pores

The total number of pores was counted on as many specimens as possible. Unfortunately, the pores on female *A. decresii* specimens were so faint (especially distally) that reliable counts could not be obtained.

The ranges and means of data for each form are shown graphically in Fig. 16. Wide overlap occurs in all forms with means of most approximating. However, the Neptune Is. sample is outstanding in the relatively low means of both sexes.

The data represented in Figs. 14–16 reflect the morphological uniformity of the complex and confirm that pore counts and the relative lengths of hind limbs and tail will not serve as useful characters for the recognition of different forms.

Discussion

Affinities of the complex

The *A. decresii* complex shows obvious affinity with two other species: *Amphibolurus rufescens* Stirling & Zietz of north-western South Australia and *A. ornatus* (Gray) of south-western Australia. Both these species are rock-dwellers agreeing with the diagnosis given above for the *A. decresii* complex except in features of coloration. The adult male of *A. ornatus* is boldly patterned dorsally with black and yellow and the tail is banded. Sexual dichromatism is not so pronounced in *A. rufescens* as in *A. ornatus* or members of the *A. decresii* complex: males lack bright colour washes about the lower jaw and throat but are bright ferruginous dorsally, matching well the colour of the rocks which they inhabit.

These two species and the *A. decresii* complex constitute a fairly well-defined and probably natural group which may be called the *Amphibolurus decresii* species-group.

Storr (1967) included *A. rufescens* as a race of *A. caudicinctus* (Günther), a species composed of several races distributed widely throughout northern, central and north-western Australia. I regard *A. rufescens* as sufficiently distinctive to merit specific rank but I do not dispute its close affinity with some races of *A. caudicinctus*. It is quite probable that the *A. decresii* species-group and *A. caudicinctus* share a common ancestry.

Figs. 10–11. *Amphibolurus fionni*. Adults in dorsal view. Fig. 10.—Holotype female from Pt. Lincoln (Area 4). Fig. 11.—Male from near Carrapateena Arm of Lake Torrens (Area 1).
Figs. 12–13. *Amphibolurus vadnappa*. Adults in dorsal view. Fig. 12.—Holotype male from Aroona Waters (Area 6). Fig. 13.—Male from Mirree Picnic Ground (Area 5).

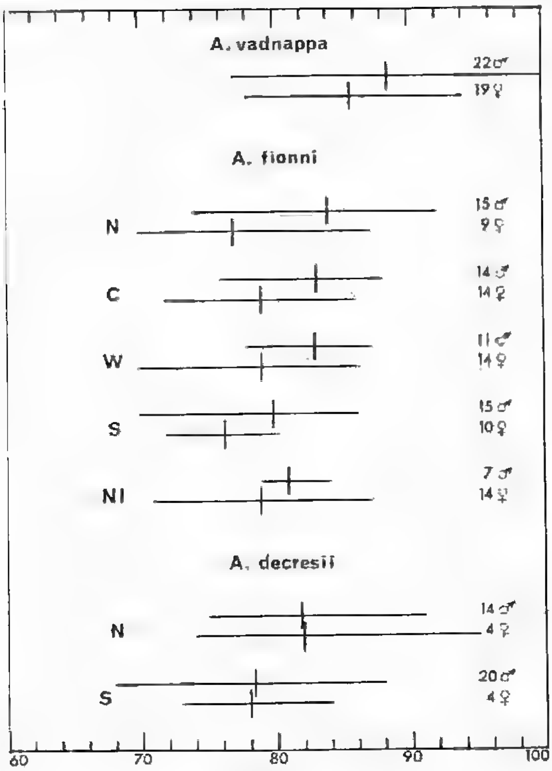

Fig. 14

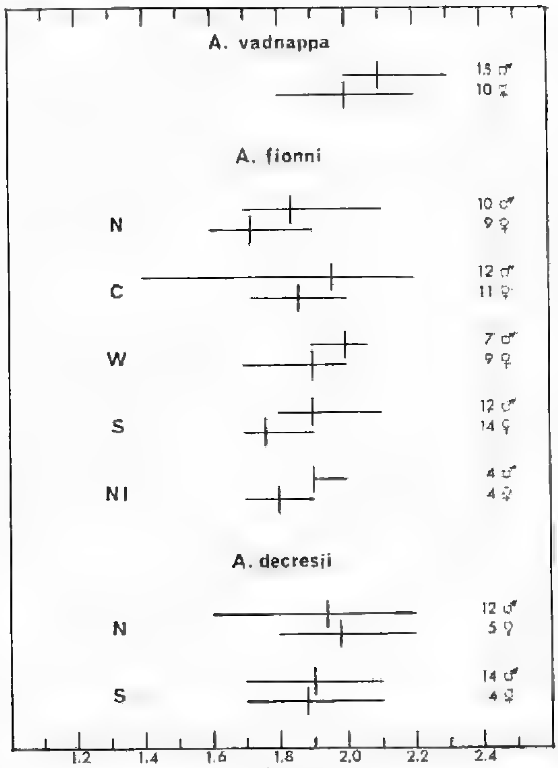

Fig. 15

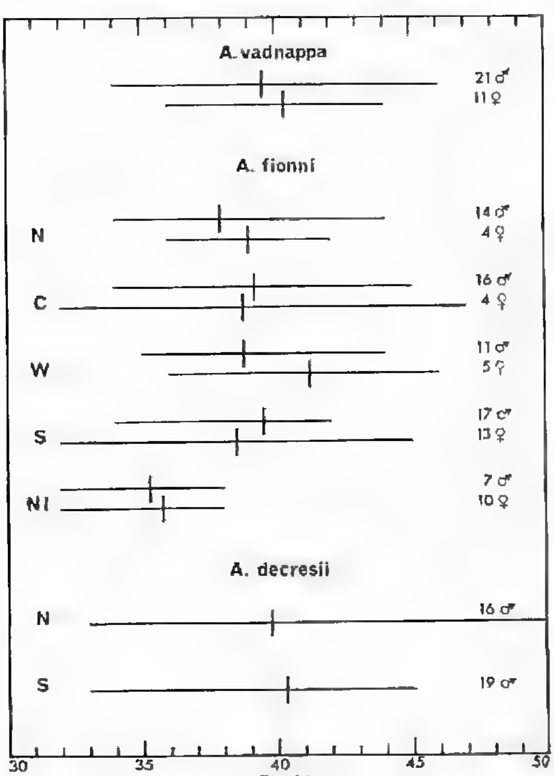

Fig 16

Fig. 14. Hind limb length as a per cent of snout-vent length in mature and near mature individuals of the *Amphibolurus decresii* complex. Ranges of variation represented by horizontal lines and means by vertical lines. Sex and sample size shown to right of each. N = northern race, C = central race, W = West Coast populations, S = southern race, NI = Neptune Is. race.

Fig. 15. Tail length as a multiple of snout-vent length in mature and near mature individuals of the *Amphibolurus decresii* complex. Explanation as for Fig. 14.

Fig. 16. Total number of femoral and preanal pores in various forms of the *Amphibolurus decresii* complex. Explanation as in Fig. 14.

Superficially, at least, there is fairly close resemblance between members of the *A. decresii* species group and *A. pictus* which inhabits chiefly sandy, shrub-dominated habitats.

Dispersal—past and present

Since the lizards of this complex appear to inhabit only rock-strewn terrain, the question arises as to how they could have colonized the many isolated hills and ranges where they now occur without having crossed wide expanses of soil plain.

While I have never seen adult and subadult specimens anywhere other than amongst rock outcrops, I have observed very small juveniles of *A. decresii* up to 100 metres away from the nearest rocks amongst dense heath and one was observed wallowing in loose sand on a bare path. This suggests that small juveniles are not behaviourally tied to rocks as are older animals and that some degree of dispersal over non-rocky terrain may be possible in the juvenile stage. I would expect, however, that the distances which such small lizards could cover would be relatively small and not sufficient to explain the colonization of hills separated by tens of kilometres of soil plain.

Because all members of the *A. decresii* species-group confine themselves to rocky habitats, I must assume that their ancestors did the same and I believe they could have dispersed over long distances only where there was sufficient rocky cover and where the gaps between outcrops did not exceed the dispersal ability of juveniles.

It is necessary to suppose, then, that rocky terrain in past times was far more extensive in South Australia than at present, providing several corridors for dragon lizard dispersal and that erosion and deposition over very long periods eventually marooned many populations as valleys widened and filled with alluvium.

I consider, too, that the lizards would not be able to cross sea barriers in the way some others are able (such as by the rafting of adults or their eggs in flood debris). The occurrence of members of the complex on several islands off the coast of South Australia appears to necessitate the assumption that the islands were once part of the mainland and that the lizards colonized them at that time.

Since the nearest living relatives of the *A. decresii* complex occur north and west of South Australia, it is likely that ancestors of the complex migrated in from those directions. Migration is unlikely to have come through the west of the State where lies the Nullarbor Plain and the sandy Great Victoria Desert, or the north-east where lies the sandy Simpson Desert. The only corridor which would have been available to the lizards lies between these deserts and is constituted by the Peake and Denison Ranges. Through these ranges the lizards could have migrated from the Musgrave and Everard Ranges, past the western side of Lake Eyre to the northern end of Lake Torrens.

This last mentioned lake and Spencer and St. Vincent Gulfs lie in the great, sediment-filled South Australian Rift Valley which is bordered along its eastern margin by the Flinders-Mt. Lofty Range system and along its western margin by the Andamooka Ranges and a series of low ranges along the eastern margin of Eyre Peninsula. Further migration may then have occurred in two separate paths, one each side of the sunklands. The eastern path probably led them south to the area now forming Kangaroo I. and a branch could have spread along the Olary Ridge (from Peterborough to the region of Broken Hill). The western path may have led south to areas of which the Neptune and Gambier Is. are now remnants.

Expansion of the lizards' range westwards possibly occurred in two areas: (1) from the hills near the junction of Lake Torrens and Spencer Gulf through the Gawler Ranges system as far west as Lake Everard, and (2) from southern Eyre Peninsula north-westwards as far as Nuyts Archipelago across a great expanse of aeolianite (limestone) country.

While the latter expanse of rock does not form any ranges, it does outcrop on low rises and in gullies. It is not necessary to suppose that this expanse was once exposed along the full length of the West Coast to explain the dragon lizards crossing it. Pockets of exposed rock, as occur today, may have expanded, coalesced, shifted and shrunken with the processes of erosion so that lizards may have been able to move from one patch to another from time to time, gradually expanding their range. The limestone sheet surrounds many granitic, gneissic and sandstone outcrops and probably provided a pathway to them.

Evolution of races

I have sought below to fit the picture of variation within the complex to the conventional concept of new forms arising through geographic isolation, although realizing that alternative explanations may be advanced.

Following colonization of major areas of South Australia by the ancestral form, changes must have arisen which rendered the area north of Lake Torrens unsuitable for habitation as it now appears to be. Thus, populations of the east were separated from those of the west by the Lake Torrens-Spencer Gulf sunklands. Perhaps coincident with these changes was the isolation of populations in the Northern Flinders Ranges from those further south. In this hypothetical situation we may envisage the independent evolution of the three main forms found today.

(a) *Amphibolurus decresii*

Because a single colour form occupies areas on both Kangaroo I. and the southern Mt. Lofty Ranges while another is found in the more northerly ranges, it must be supposed that a barrier to dispersal existed between the North and South Mt. Lofty Ranges well before the separation of Kangaroo I. by the formation of Backstairs Passage. The area now, between Gawler and Kapunda, consists of very low rolling hills which do not provide any suitable outcrops for habitation by *A. decresii*.

The widening and filling of valleys between individual ranges and hills has isolated many populations in the more northerly parts of the range of this species and, presumably as a result, a minor degree of diversity in coloration has arisen amongst them.

(b) *A. fionni*

The present distribution of male colour forms suggests isolation occurred of populations in Areas 1, 2, 3–4 (Fig. 1) and on Neptune and Wedge Is. allowing genetic divergence to develop.

Since the populations of Neptune and Wedge Is. show strong differences from those of the near mainland, it may be suggested that these islands were separated (by the sea level rising in relation to the land) much earlier than islands to the north-west, where populations appear more like those of the near mainland. The generally deeper waters surrounding Neptune and Wedge Is. give some credence to this theory. However, it could also be suggested that there are some differences in the habitats occupied on these islands which exerted strong selective pressures and brought about changes in the inhabitants whereas the habitats of the north-west islands were much the same as those of the mainland.

Two barriers to dispersal must have arisen on the mainland: one north-west of Pt. Augusta (separating area 1 from 2) and another on southern Eyre Peninsula (isolating area 2 from area 3-4). In these two areas development of rocky terrain was presumably weaker than elsewhere so that the processes of erosion and deposition were able to break down or bury the rocks over a sufficiently wide area to disrupt dispersal.

As time went on, this process continued within each area splitting off more and more isolates. Even very small populations may show evidence of their isolation. For example, an unusually bold colour pattern characterises females from the Marble Range.

(c) *A. vadnappa*

Only one major barrier to dispersal of this species appears to have arisen: a broad tract of sandy country passing through Farina and separating the Willouran Ranges from the northern Flinders Ranges.

Perhaps subsequent to the formation of this gap, the barrier separating *A. decresii* from *A. vadnappa* was overcome by the former, thus allowing colonization of the eastern part of the range of the latter. I am at a loss, however, to suggest just how this could have come about.

The evolution of the *A. decresii* complex, as envisaged above, parallels the model of speciation proposed by Pianka (1972) for habitat-restricted lizards living in "shrub-*Acacia*" or "sandplain-*Triodia*" habitats: in both cases, habitats fluctuating in space and time are believed to be the key factor.

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